Phenology and natural mortalities of the fir needleminer, *Epinotia fraternana* (Hw.) (Lepidoptera, Tortricidae)

MIKAEL MÜNSTER-SWENDSEN

Münster-Swendsen, M.: Phenology and natural mortalities of the fir needleminer, *Epinotia fraternana* (Hw.) (Lepidoptera, Tortricidae).
Ent. Meddr 57: 111-120. Copenhagen, Denmark, 1989. ISSN 0013-8851.

The phenology and natural mortalities were investigated by use of funnel traps, emergence traps, branch samples and forest litter samples in a plantation of *Abies nordmanniana* (Stev.). Larval endoparasitism constituted 81.6% in 1986 and 78.8% in 1987. *Charmon extensor* (Linn.) (Braconidae) was the predominant primary parasitoid followed by *Pimplopterus dubius* (Hlmg.) (Ichneumonidae). Apparently, neither of these are host-specific, but they seem to show a delayed density dependent response to *E. fraternana*. Ectoparasitism of 18.4% and 23.7% and a predation by cecidomyid larvae of 1.7% on mining larvae were recorded. 25.3% of the hibernating larvae were killed by the pathogenous fungus *Paecilomycis farinosus* (Holm), whereas at least 15.3% of the hibernating larvae and pupae were killed by predators, possibly by *Athous subfuscus* L. (Elateridae) and some staphylinids. The phenology and the sequence and magnitude of mortalities were almost identical with those of *Epinotia tedella* (Cl.), a closely related needleminer in Norway spruce, and so was the pattern of population fluctuations. Only the attachment to different host tree genera seems to separate the two species ecologically.

Hence, key factors and predictive models of *E. tedella* may to some extent be valid for *E. fraternana* also.

M. Münster-Swendsen, Institute of Population Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark.

Introduction

Epinotia fraternana (Hw.) (syn. *E. proximana* H.S.) (Lepidoptera: Tortricidae) is known as a pest insect on fir (*Abies* sp.) in Europe (Oudemans 1932, Patocka 1960, Bejer 1986, Münster-Swendsen 1978a). The species is most abundant in south-eastern Europe, and is there giving rise to serious defoliations in fir forests (Patocka 1960, Sorauer 1953). In Denmark the species is mainly regarded as a pest in Christmas greeneries (on *A. nordmanniana* (Stev.) and *A. procera* Rehd.), where the appearance of young trees are of economic importance (Bejer 1986).

E. fraternana has a biology very similar to that of the spruce needleminer, *Epinotia tedella* (Cl.), except for its host tree. Thus, *E. fraternana* is restricted to the genus *Abies*, whereas *E. tedella* is restricted to the genus *Picea* (Münster-Swendsen 1978a). Due to similarities in morphology and biology there has earlier been some confusion in the identification of the cause of mine damages on fir plantations (Bejer 1986), but the choice of host tree and the method of mining and of spinning hollowed needles together make it easy to avoid mistakes (Münster-Swendsen 1978a).

In Denmark the fir needleminer seems to have population fluctuations that coincide with those of the spruce needleminer, judged by the damage reports (Bejer 1986). The influence of precipitation on the condition of spruce trees and, through this, also on survival and fertility of the spruce needleminer has been studied (Münster-Swendsen 1987a) and short and long term models of prognosis have been introduced (Münster-Swendsen 1987b). Since the dynamics of *E. fraternana* may be controlled in a way similar to *E. tedella*, the knowledge of population dynamic functions and the method used in prognosis may be transferred from the latter to the former species.

In order to validate a comparison between the two species with regard to fluctuations, regulation and prediction of severe damage, the phenology and the sequence and magnitude of natural mortalities of the fir needleminer, *E. fraternana* was studied during the years 1986 and 1987 in north Zealand, Denmark.

Material and Methods

The investigations were performed in a 20 year old plantation of *Abies nordmanniana* (Stev.) at the Strødam Reserve. The plantation was rather irregular and mixed with young birch trees.

Emergence of adult fir needleminers and their parasitoids were studied by use of emergence traps covering 1/8 m^2 each, described in Münster-Swendsen (1973). The traps were placed on the forest floor from mid April to the beginning of July and attended weekly.

Ten plast-foil funnels, each covering 0.65 m^2, were placed under the crowns of ten trees to catch the larvae spinning down from October to December. The yields were collected weekly and the larvae (247 in all) counted and dissected for the study of parasitism.

15 branch samples were taken in September and October both years, and the distribution of fresh mines and larval mortality in mines were studied. Besides, live larvae were dissected to maximize the total number of larvae (305 specimens) investigated for endoparasitoids.

The connection between different types of endoparasitoid larvae and identified adult parasitoids was assessed by comparing parasitoid frequencies in larval samples and in samples of larvae that were kept in the laboratory until emergence of both moths and adult parasitoids.

Twenty-one 0.08 m^2 samples of litter and raw humus were extracted by use of Berlese funnels for the study of potential predators of larvae and pupae of *E. fraternana*. Litter and raw humus covered by the emergence traps were searched through after the emergence of adults had ceased, and all remaining cocoons were studied in order to identify the causes and frequencies of mortalities. This involved the growth of fungi from dead larvae on malt-agar.

Forty-seven adult moths caught in emergence traps were dissected in the search of protozoan pathogens, but none was found.

Results and Discussion

Phenology and relation to needle age

The adults emerge in June and no protandry was observed. In 1987 about 5% of the adult population had emerged on 5 June, 50% on 19 June, and on 6 July 97% had emerged (n = 97 specimens) (see Fig. 1b).

Eggs are deposited singly on the needles, and larvae are mining in needles during the autumn. The larva mines 3-4 neighbouring needles kept together by silken threads, then moves to another site and mines 3-4 needles. In total, about 12 needles are mined by each larva (Münster-Swendsen 1978a).

The mines of *E. fraternana* are mainly found on branches with a low and shaded position in the crown. The distribution of 180 mines was recorded with respect to the age of shoots and needles. Fig. 2 shows that

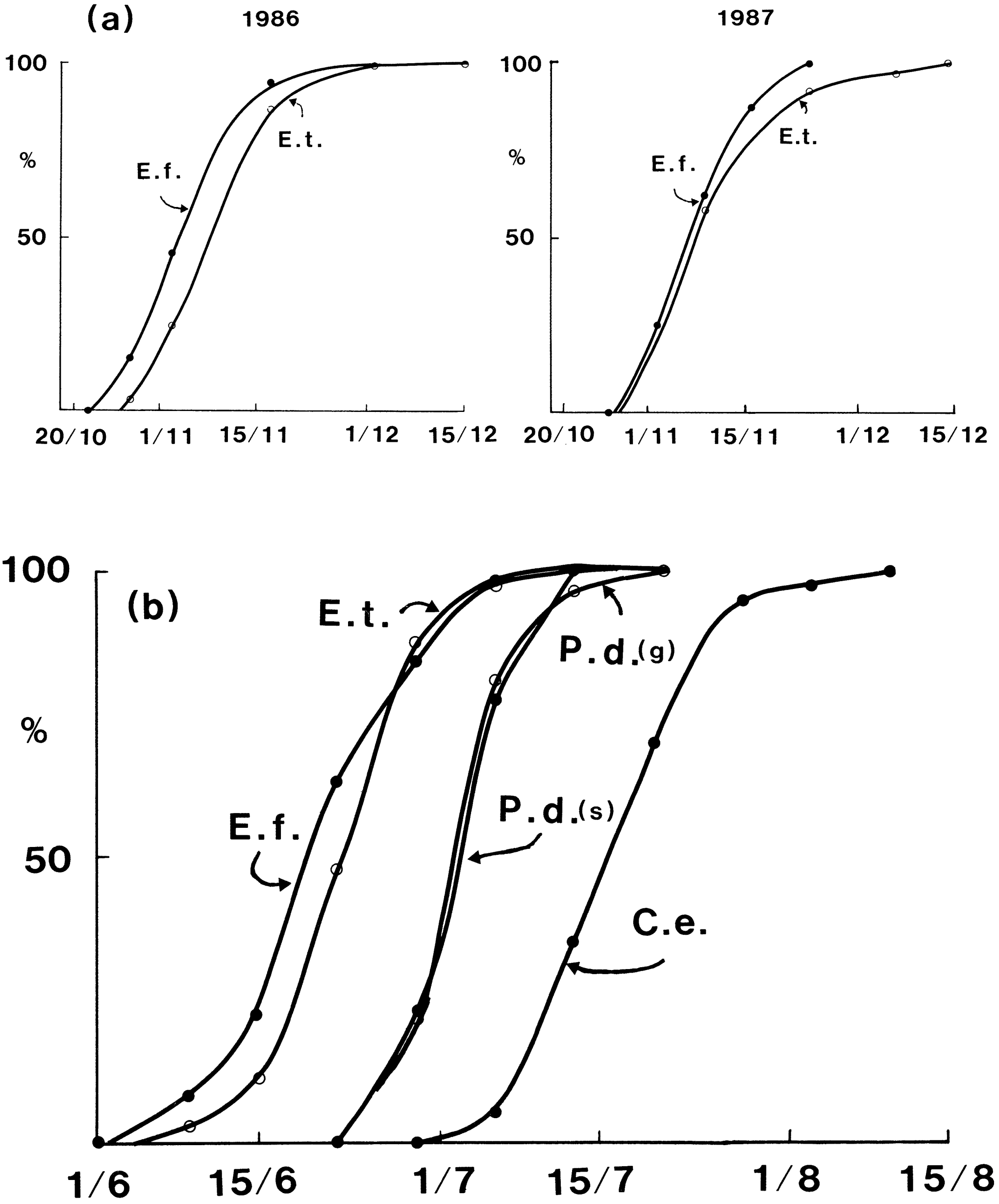


Fig. 1. Phenology of *E. fraternana* (E.f.) compared with *E. tedella* (E.t.). (a) Cumulated frequency of larvae spinning down from the canopy in 1986 and 1987. (b) Cumulated frequency of adult emergence in 1987 of *E. fraternana* (E.f.), *C. extensor* (C.e.), and of *P. dubius* in the fir stand at Strødam (P.d.(s)) and in the spruce stand at Gribskov (P.d.(g)).

Fig. 1. Fænologi hos E. fraternana *(E.f.) sammenlignet med* E. tedella *(E.t.). (a) Kumuleret hyppighed af nedfirende larver i 1986 og 1987. (b) Kumuleret hyppighed af klækning af voksne i 1987 hos* E. fraternana *(E.f.),* C. extensor *(C.e.) og hos* P. dubius *i ædelgran-bevoksning i Strødam (P.d.(s)) og i rødgran-bevoksning i Gribskov (P.d.(g)).*

shoots of the current year are avoided and that two-year-old shoots (or needles) are preferred as mining sites. However, as young shoots are more numerous than older shoots on a branch, the preference for old shoots is even more pronounced than indicated by the distribution in Fig. 2.

In November, healthy and parasitized larvae spin down by silken threads to hibernate in cocoons in the forest floor. The temporal distribution of descending larvae was studied in 1986 and 1987. Fig. 1a shows that descent commenced after 22 October in 1986 and after 26 October in 1987. 50% had descendence on 4 November in 1986 and on 7 November in 1987. In both years all larvae had spun down by the end of November.

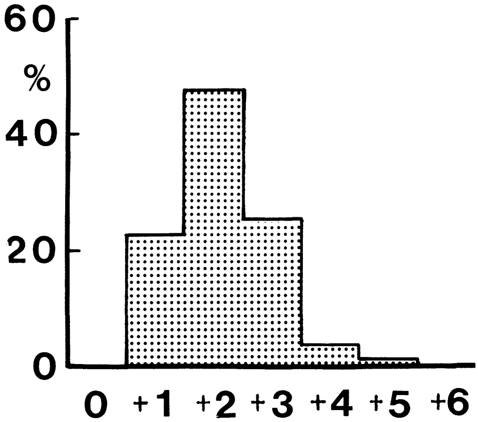


Fig. 2. Frequency distribution of 180 mining *E. fraternana* larvae on shoots of different age. 0 = current year shoots, +1 = shoots of previous year, +2 = two-year-old shoots, etc.

Fig. 2. Fordeling af 180 minerende E. fraternana-*larver på skud af forskellig alder. 0 = indeværende års skud, +1 = skud fra foregående år, +2 = to år gamle skud osv.*

Natural mortalities

Mortalities of larvae in their mines were recorded during two generations (autumns 1986 and 1987), and mortalities of prepupae and pupae resting in the forest floor were recorded in one generation (spring 1987). The sequence of mortalities was as follows: 1) young larvae (L_1 and L_2) are attacked by endoparasitoids in July and August, but the parasitoid larvae do not kill their host larvae until the following spring, 2) both healthy and parasitized larvae (L_3 and L_4) are attacked and killed by either ectoparasitoids or cecidomyid larvae in September-October, 3) prepupae resting in the forest floor may be killed by a pathogenous fungus in April-May, and 4) prepupae and pupae may be killed by predators in May. Adult mortalities and egg mortalities were not studied.

Endoparasitism

The degree of parasitism was studied by dissection of larvae from both branch- and funnel samples, whereas ectoparasitism and mortality due to cecidomyids were recorded by investigations of mines in branch samples. The frequency of the various parasitoid larval types was studied by dissections, and through consecutive emergence of adult parasitoids from identical samples the identities of adult and larval species were assessed.

Larval endoparasitism was found to be 81.6% in 1986 and 78.8% in 1987. In both years *Charmon extensor* (Linn.) (Braconidae) was predominant and gave rise to 64.9% and 69.7% parasitism, respectively. Next, *Pimplopterus dubius* (Hlmg.) (Ichneumonidae) caused 16.2% and 9.1% parasitism, and *Apanteles* sp. (Braconidae) 0.5% and 0.0%, respectively.

C. extensor showed extensive superparasitism with up to four larvae in one host, but analysis of data from 1987 resulted in a distribution of offsprings per host larva that followed a Poisson series, i.e., superparasitim may be a result of no discrimination between healthy and already parasitized hosts and of random search by the ovipositing parasitoid.

The number of hosts containing both *C.*

extensor and *P. dubius* did not differ from the number expected by a random overlap, i.e., it indicates lack of multiparasitic avoidance or attraction. However, by such multiparasitism *P. dubius* was always found as the looser of the interference competition, being encapsulated by host haemocytes and dead. Thus, the original parasitism due to *P. dubius* must have been about 46% in 1986 and 30% in 1987, and only multiparasitism and take-over by *C. extensor* reduced the host larvae containing a live *P. dubius* to 16.2% and 9.1%, respectively.

The emergence of *P. dubius* and *C. extensor* (see Fig. 1b) was recorded by emergence traps in the field in 1987. *P. dubius* showed a delay of about 13 days compared with the emergence of its host and coincided closely with the emergence of *P. dubius* having parasitized *Epinotia tedella* (Cl.) in a spruce plantation in a nearby forest. The emergence of *C. extensor* showed a delay of 27 days, compared with its host, and a female ratio of 0.625 (n = 40). Apparently, *C. extensor* attacks the host somewhat later than do *P. dubius*.

It was noted that the developing gonads of descending, parasitized larvae were heavily suppressed. Since healthy male gonads are easily detected as light brown spots on fully grown larvae - and as the host sex ratio is close to 1:1 and the parasitoids do not discriminate between host sexes - the degree of parasitism may be estimated through observation of the frequency of larvae with normally developed male gonads. As an example: if 20% of the larvae show normal male gonads, the degree of parasitism is (100 - (2 x 20)) = 60%. In 1986 parasitism estimated by this method was 80.1%, while subsequent dissections showed a true parasitism of 81.6%.

Ectoparasitism

Ectoparasitism, i.e., parasitoids depositing their eggs outside the integument of the mining larvae, was abundant both years. The percentages of larvae killed by ectoparasitoids were 18.4% in 1986 and 23.7% in 1987. A few adult wasps emerging from mines in the laboratory were identified as *Bracon* sp., but other species may as well be involved in ectoparasitism of *E. fraternana*. Thus, the ectoparasitoid *Scambus brevicornis* (Grav.) (Ichneumonidae) emerged in considerable numbers within the fir stand during early spring. Since no *E. fraternana* larvae are available in the spring, *S. brevicornis* may parasitize one or more other host species. Accordingly, a few specimens were found in *Argyresthia fundella* F.R. (Yponomeutidae), the larvae of which are mining in fir needles during the spring (Münster-Swendsen 1978b).

Obviously, both healthy and endoparasitized larvae were attacked by ectoparasitoids, and ectoparasitized larvae were always found immobile - apparently paralyzed by the ovipositing ectoparasitoid. Larvae parasitized by ectoparasitoids all died in their mines during late autumn.

Predation by cecidomyid larvae

A small portion (1.7% in 1987) of the mining larvae was attacked and killed by predacious cecidomyid larvae. The cecidomyid larvae were very alike and may all belong to one species, but they were never identified. Both healthy and parasitized larvae were attacked and killed.

Mycosis

Investigations of 155 cocoons resting in the soil after adult emergence revealed that some larvae, and a few pupae, had been killed by fungus disease during hibernation. Mortality due to mycosis was 25.3% in the spring of 1987, and both parasitized and unparasitized larvae were found to be killed by the fungus. By breeding the fungi on malt-agar plates and on larvae of *Agrotis segetum*

(Den. & Schiff.) (Noctuidae), the responsible pathogenous fungus was identified as *Paecilomyces farinosus* (Holm).

Soil predation

The mortality due to predation of larvae and pupae in their cocoons was difficult to measure, since dead larvae or pupae must be found in the cocoons in order to identify the cause of death. The investigations gave a rough, possibly underestimated, figure of 15.3% mortality.

The predators responsible are not known for sure, but extractions from 21 litter samples showed a density of the predacious elaterid *Athous subfuscus* L. of 17.3 ± 5.1 (S.E.) larvae per m^2 and a density of predacious staphylinids (mainly of the genera *Othius* and *Philonthus*) of 37.3 ± 5.6 (S.E.) adults and larvae per m^2.

Bionomics compared with *Epinotia tedella*

Fig. 1 shows that the phenology of the two *Epinotia* species is practically identical. This means that the weather conditions of a given period may have identical impact on both species, both directly and through the influence on the host trees.

The distribution of mines on the host tree is similar for the two species since also *E. tedella* prefers the low and central parts of the crown as mining sites (Münster-Swendsen 1980). The distribution of *E. tedella* mines on shoots, or needles, of different ages also shows a preference for shoots more than two years old (Münster-Swendsen unpublished). Thus, it seems likely that the effect of host tree condition on insect condition and dynamics in *E. fraternana* may follow that of *E. tedella* (Münster-Swendsen 1987a), i.e., low precipitation in May-September leads to a low growth and resistance in the trees and hence to a fine condition of the larvae mining during the autumn. This, in turn, leads to a low mortality during hibernation and to a high fertility of the adults in the following spring.

The sequence and magnitude of mortalities of *E. fraternana* resemble very much those of *E. tedella.* Table 1 presents the results for *E. fraternana* and *E. tedella* in 1986-87 and average figures of the period 1970-79 for *E. tedella* (Münster-Swendsen 1985 and unpublished). It may be noted that the causes of mortalities are almost identical.

The frequency of endoparasitism was very high for both species in 1987. In case of *E. tedella* this was a result of a gradual increase of the population during the previous years and a consequtive increase of the parasitoid populations (Münster-Swendsen 1987a). A similar increase of parasitism may also have taken place in *E. fraternana.* According to damage reports (see Fig. 3) *E. fraternana* also had high population densities in the previous years.

Both *P.dubius* and *C. extensor* are known as members of the parasitoid complex of *E. tedella* (Schedl 1951, Capec et al. 1969). In Denmark, *P. dubius* is one of two dominating primary parasitoids, whereas *C. extensor* is only rarely found in *E. tedella* (Münster-Swendsen 1979).

Routine samplings of *E. tedella* by the author showed that ectoparasitism was also abundant in 1987 in this species. The parasitoid species involved may be different for the two host species. Thus, *Dipriocampe* sp. (Tetracampidae) has been found on *E. tedella* (Münster-Swendsen 1979). Normally, the level of ectoparasitism is very low (0-2%) in *E. tedella* (Münster-Swendsen 1987a).

Mycosis due to *P. farinosus* is found every year in hibernating *E. tedella.* The frequency of attacked larvae varies according to the density of attacked *E. tedella* larvae in the previous generation that remain in the forest floor, and to the state of health of the larval population descending from the trees (Münster-Swendsen 1985, 1987a). Whether the interaction between this pathogenous fungus and *E. fraternana* is of a similar kind is not known, but quite expectable.

Athous subfuscus is the predominant predator in hibernating larvae and pupae of *E. tedella* (Münster-Swendsen 1985). However, in a spruce stand with a well developed raw humus layer the density of *A. subfuscus* is much higher (above 100 larvae per m^2 (Münster-Swendsen unpublished)) than in the present fir stand. The fir stand at Strødam has a rather thin, raw humus layer and - maybe also for other reasons - a low density of *A. subfuscus* larvae. Yet, other predators, such as the abundant staphylinids, may exert a significant mortality in *E. fraternana.*

Total generation mortality was rather similar for both species, and so was the decrease from 1986 to 1987 in density of larvae spinning down. Thus, the density of descending *E. fraternana* larvae was 26.8 per m^2 in 1986 and 24.6 per m^2 in 1987. This population decline of 90.8% may be compared with a simultaneous decline in *E. tedella* of 86.3% and 96.6% (in two stands). Since the mortalities of the two species were of similar size in 1986-87 and the population declines were also of the same magnitude, there are reasons to believe that the fertility has also been similar for the two species.

Population dynamics

In Denmark, the dynamics of *E. tedella* has been studied since 1970 (Münster-Swendsen 1987a), whereas for *E. fraternana* only damage reports are available. Population fluctuations in *E. tedella* are compared with the frequencies of damage reports for both species in Fig. 3 (files of damage reports disposed by B. Bejer). Years with notable damage seem to correspond for the two species and with the population curve for *E. tedella.*

The heavy decline in population of *E. tedella* from 1986 to 1987 was apparently due to a high degree of parasitism following the high host population densities in 1985, and to significant precipitation during the summer months of 1985 (and 1987) affecting the host trees in a positive way (Münster-Swendsen 1987a). Since damage- and population maxima of the two species correspond

Table 1. Sequence and magnitude of mortalities in *E. fraternana* and *E. tedella.* (A) and (B) refer to two different spruce stands and (M) to average figures from one stand. Egg mortality in *E. tedella* was due to the parasitoid *Trichogramma* sp. Generation mortality does not include adult mortality and, for 1986-87, egg mortality. In 1986-87, mycosis and predation were just measured as total winter mortality in *E. tedella.*

Tabel 1. Rækkefølge og størrelse af mortaliteter hos E. fraternana *og* E. tedella. *(A) og (B) er resultater fra to forskellige rødgran-bevoksninger og (M) er gennemsnitstal fra én bevoksning. Ægmortalitet hos* E. tedella *skyldes parasitoiden* Trichogramma *sp. Generationsmortalitet indeholder ikke voksenmortalitet og, for 1986-87, ægmortalitet. I 1986-87 blev mykose og predation blot målt som samlet vintermortalitet hos* E. tedella.

	E. fraternana 1986-87	*E. tedella* 1986-87 (A)	*E. tedella* 1986-87 (B)	*E. tedella* 1970-79 (M)
Egg mortality	?	?	?	15.8%
Endoparasitism	78.0%	72.6%	66.9%	51.8%
Ectoparasitism	18.4%	?	16.0%	0-2%
Mycosis	25.3%	73.9%	81.7%	27.4%
Predation	c. 15.3%			46.4%
Generation mortality	88.7%	92.9%	94.0%	84.1%

so well, and since they both show a heavy parasitism in 1986, the dynamics and key factors for fluctuations may be very similar in both *Epinotia* species. This means that the varying condition of the host trees (food quality and secondary substances) due to precipitation and a delayed density dependent parasitism may be the key factors in *E. fraternana*, as they are in *E. tedella* (Münster-Swendsen 1987a).

Predictions

The above mentioned key factors have been applied in a short and long term predictive model for *E. tedella* (Münster-Swendsen 1987b), and a similar predictive model may fit to *E. fraternana* as well. However, the precise mathematical description of the relationship between *E. tedella* and its host tree condition, or previous precipitation, and the model of parasitism used in long term predictions are based on analysis of field data from investigation of *E. tedella* populations (Münster-Swendsen 1985, 1987b) and may possibly not be directly transferred to *E. fraternana* populations.

A prediction of population changes in *E. fraternana* in the years to come may be based on the facts that 1) it has a pattern of fluctuations close to that of *E. tedella*, 2) both species showed a population decline of similar magnitude from 1986 to 1987, and 3) both had a high degree of parasitism in November 1987. Due to this and the heavy precipitation in the summer of 1987, a very low population density was expected in the autumn of 1988 and, as it takes some years to build up a high density, the next population maximum should not appear until the beginning of the nineties – irrespective of weather conditions.

To conclude, *E. fraternana* has a biology, phenology and a sequence of mortalities almost identical with those of *E. tedella* and, apparently, this leads to identical dynamic patterns in the two species. Thus, the dominant ecological difference between the two *Epinotia* species is their association with two different host tree genera.

Acknowledgements

The author would like to thank the committee of the Strødam Reserve for the access to the research area, and B. Bejer, The Royal Veterinary and Agricultural University, Copenhagen, for the disposal of damage reports.

Sammendrag

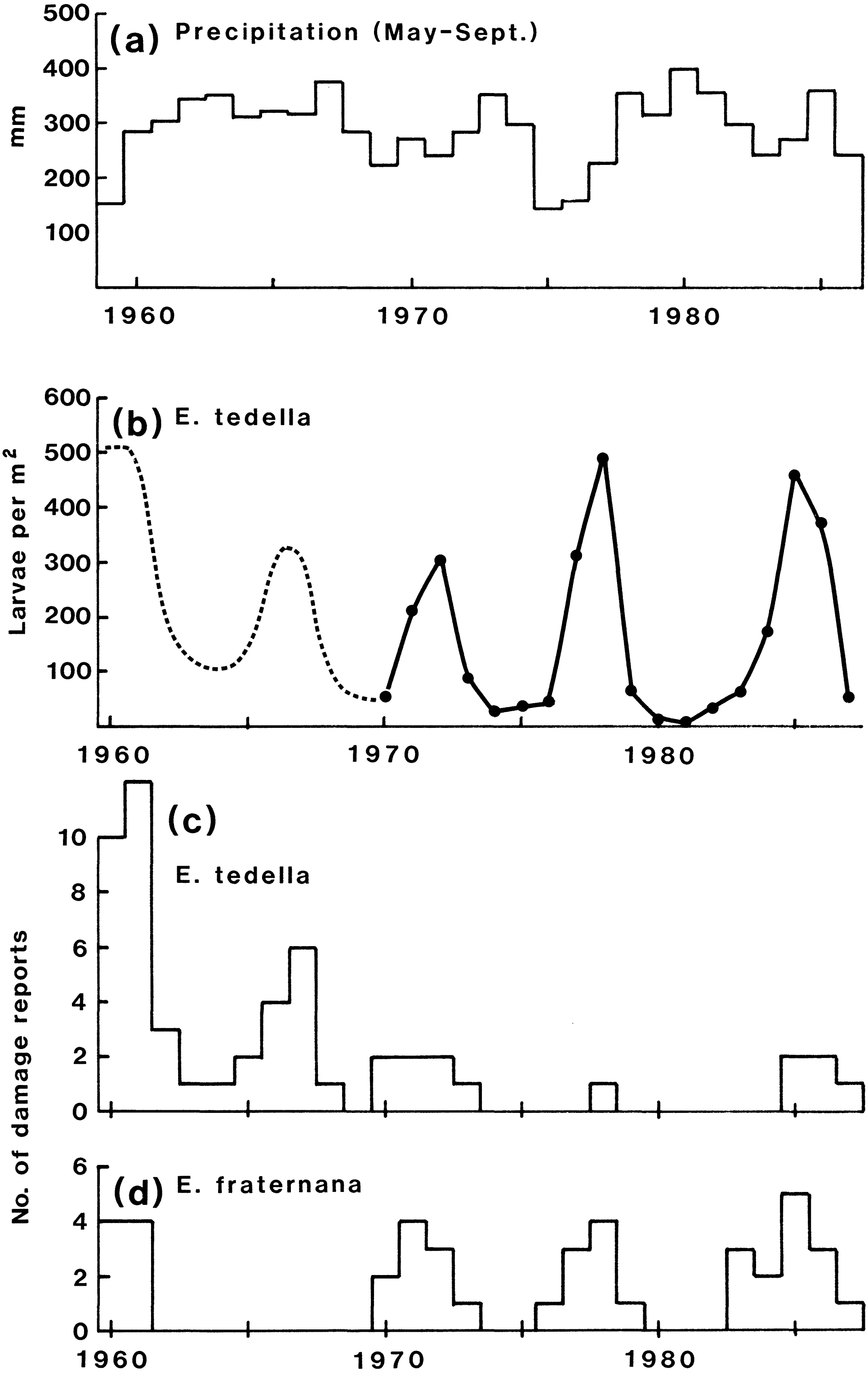
Fænologi og naturlige mortaliteter hos ædelgrannålevikleren, *Epinotia fraternana* (Hw.) (Lepidoptera: Tortricidae).

Fænologi og naturlige mortaliteter blev i 1986 og 1987 undersøgt ved brug af tragtfælder og klækkefælder, samt gennem prøver af grene og skovbundens førnlag.

Snyltehvepse havde i 1986 parasiteret 81,6%, og i 1987 78,8%, af larverne. *Char-*

Fig. 3. Precipitation (May-September) (a) and fluctuations of larval density in *E. tedella* (b) and of frequency of damage reports due to *E. tedella* (c) and to *E. fraternana* (d). The time axis of precipitation is displaced one year compared with the population curve and damage reports, since the effect of precipitation on population changes are delayed. The broken line in (b) represents assumed population fluctuations based on damage reports (c) and the observed oscillations in 1970-87.

Fig. 3. Nedbør (maj-september) (a) og svingninger i larvetæthed hos E. tedella *(b) og i hyppighed af skadeanmeldelser for* E. tedella *(c) og for* E. fraternana *(d). Tidsaksen for nedbør er forskudt ét år i forhold til populationskurven og skadeanmeldelserne, da nedbør indvirker på populationsændringerne med en vis forsinkelse. Den stiplede linje i (b) repræsenterer de formodede populationssvingninger baseret på skadeanmeldelser (c) og de observerede oscillationer i 1970-87.*


(a) Precipitation (May-Sept.)
mm
500
400
300
200
100
1960
1970
1980
(b) E. tedella
Larvae per m²
600
500
400
300
200
100
1960
1970
1980
(c)
E. tedella
No. of damage reports
10
8
6
4
2
0
(d) E. fraternana
6
4
2
0
1960
1970
1980

mon extensor (Linn.) (Braconidae) var den dominerende parasitoid efterfulgt af *Pimplopterus dubius* (Ichneumonidae). Formentlig er ingen af disse snyltehvepse værtsspecifikke, men de synes alligevel at vise en forsinket tæthedsafhængig respons over for *E. fraternana* og dermed en vis regulering af viklerbestanden.

18,4% og 23,7% af larverne – med eller uden endoparasitoid-larver i – blev angrebet af ektoparasitoider af slægterne *Bracon* (Braconidae) og *Scambus* (Ichneumonidae), og 1,7% blev dræbt af prædatoriske galmyg-larver (Cecidomyiidae).

Under overvintring i skovbunden blev 25,3% af larverne dræbt af den insekt-patogene svamp *Paecilomyces farinosus* (Holm), mens mindst 15,3% af de overlevende larver og pupper blev dræbt af prædatorer (*Athous subfuscus* L. (Elateridae), samt forskellige staphylinider).

Fænologi samt rækkefølge og størrelse af mortaliteter blev sammenlignet med den nærtbeslægtede vikler *Epinotia tedella* (Cl.), der minerer på rødgran. De to arter viste sig næsten identiske med hensyn til disse forhold, samt populationernes fluktuationer. Kun deres tilknytning til forskellige værtstræ-slægter (*Abies* versus *Picea*) synes at adskille dem økologisk. Således kan kendskab til nøglefaktorer, fluktuationsmønstre og prognosemodeller for *E. tedella* formentlig også anvendes over for *E. fraternana*.

References

Bejer, B., 1986: Insektskader på nåleskov i Danmark. En historisk oversigt. – Det forstlige Forsøgsvæsen i Danmark 40: 225-237.

Capec, M., Kristek, J. & Oehlke, J., 1969: Zur Problematik der Insektenparasiten des Fichtennestwicklers *Epinotia tedella* (Cl.). – Acta Univ. Agric. Brno. Rada C 38: 271-283.

Münster-Swendsen, M., 1973: En klækkefælde og en faldgrubefælde til insekt-økologiske undersøgelser. – Flora og Fauna 79: 85-92.

– 1978a: Ædelgrannålevikleren (*Epinotia proximana* H.S.), et skadedyr i pyntegrøntkulturer. – Dansk Skovf. Tidsskr. 63: 309-315.

– 1978b: Ædelgrannålemøllet (*Argyresthia fundella* F.R.), et potentielt skadedyr. – Dansk Skovf. Tidsskr. 63: 254-261.

– 1979: The parasitoid complex of *Epinotia tedella* (Cl.) (Lepidoptera: Tortricidae). – Ent. Meddr 47: 63-71.

– 1980: The distribution in time and space of parasitism in *Epinotia tedella* (Cl.) (Lepidoptera: Tortricidae). – Ecol. Entom. 5: 373-383.

– 1985: A simulation study of primary-, clepto-, and hyperparasitism in *Epinotia tedella* (Lepidoptera: Tortricidae). – J. Anim. Ecol. 54: 683-695.

– 1987a: The effect of precipitation on radial increment in Norway spruce (*Picea abies* Karst.) and on the dynamics of a lepidopteran pest insect. – J. Appl. Ecol. 24: 563-571.

– 1987b: Gode prognoser for grannålevikler-angreb – indtil videre. – Skoven 19: 96-98.

Oudemans, J.T., 1932: *Epiblema proximana* H.S., een nieuwe vijand onzer Naaldboomen. – Entom. Ber. 8: 342-346.

Patocka, J., 1960: Die Tannenschmetterlinge der Slowakei. – 215 pp. (Bratislava).

Schedl, K.E., 1951: Der Fichtennestwickler (*Epiblema tedella* (Cl.)). – 136 pp. Landesforstinspektion für Kärnten, Bodensdorf.

Sorauer, P., 1953: Handbuch der Pflanzenkrankenheiten. Band 4. – 518 pp. (Berlin).